Predation on intertidal mussels

Waser, A.M.

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9 | General discussion

Andreas M. Waser

The work presented in this thesis was part of two major research projects ('Mosselwad' and 'Waddensleutels'), exploring the need and the possibilities for mussel bed restoration in the Dutch Wadden Sea. The aim of the work was to investigate how predation on intertidal mussels affects the survival of littoral beds. The findings of this thesis supplement previous work that focussed on other aspects affecting the stability of intertidal mussel beds in the Dutch Wadden Sea (Donker 2015, de Paoli 2017). In this final Chapter, the main results and conclusions are summarized and their implications for mussel bed restoration measures are discussed.

Regional differences in predation pressure on intertidal mussels

Mussel beds are a common habitat feature throughout the Wadden Sea (Dijkema et al. 1989, Dijkema 1991, Folmer et al. 2014). Areas with low exposure to tidal currents and waves offer the most favourable conditions for littoral mussel beds and show highest mussel bed coverages in the Wadden Sea (Folmer et al. 2014). The coverage of mussel beds in the different Wadden Sea regions is subject to considerable year-to-year variations, which cannot entirely be explained by environmental conditions such as cold winters and storms (Folmer et al. 2014). Amongst other things, predation pressure on intertidal mussels is one of the potential factors affecting the short-term dynamics of mussel beds.

Predation pressure on a given mussel bed largely depends on the local predator abundances. All size classes of mussels on intertidal mussels beds are subject to predation by a suite of predators, most notably shore crabs and shellfish-eating birds (Zwarts & Drent 1981, Smallegange & van der Meer 2003, van de Kam et al. 2004). A comparison of waterbird abundances corrected for the surface area of specific foraging habitats among the tidal basins of the Dutch and German Wadden Sea, revealed pronounced differences in bird density between the different Wadden Sea regions (**Chapter 2**). These patterns were also manifested in the shellfish-eating birds, showing high densities in the western Dutch Wadden Sea and in the south of Schleswig-Holstein and lower densities in the eastern Dutch Wadden Sea, in Lower Saxony and in the north of Schleswig-Holstein. These area corrected bird abundances only allow a general comparison of predation pressure on the benthos among the different Wadden Sea areas. A thorough analysis of predation pressure, requires comprehensive information on prey distribution and prey quality. Extensive sampling of the macrobenthos is only performed in the Dutch Wadden Sea, such as a grid-point survey designed for the macrobenthic species on the tidal flats (Compton et al. 2013) and surveys focussing on commercially important bivalves (e.g., mussels, cockles; van den Ende et al. 2016b, van Asch et al. 2016). In Germany, no such area-wide surveys exist, which hampers efforts to compare the predation pressure between the different Wadden Sea regions.

Furthermore, for an overall comparison of predation pressure on mussels at intertidal bivalve beds in the different Wadden Sea regions, the abundance of other mussel predators (i.e. shore crabs) should also be considered. However, current monitoring programmes that survey annual abundances of fish and epibenthic macroinvertebrates (e.g., crabs, shrimp) throughout the Wadden Sea (Demersal Fish Survey (DFS) in the Netherlands and Demersal Young Fish Survey (DYFS) in Germany) are hardly capable of identifying differences of shore crab abundance among different intertidal areas. This is mainly because these surveys are restricted to tidal channels and gullies deeper than 2 m (e.g., Tulp et al. 2012; 2016) and presumably can only give inadequate information of the intertidal crab population. Moreover, the surveys in the Dutch and German Wadden Sea differ slightly in their sampling methodology. While in the Dutch DFS beam trawls are equipped with a tickler chain and therefore can catch epibenthic organisms more efficiently, trawls in the German DYFS programme do without extra chains (e.g., Tulp et al. 2016). Up to date differences in catching efficiency between the two beam trawl types are not well known, making comparisons of the two surveys complicated (Tulp et al. 2016). Focussing only on the Dutch DFS, however, no explicit differences in shore crab abundance

in subtidal areas are apparent between the western and eastern Dutch Wadden Sea (Tulp et al. 2012). Assuming that no substantial differences in the relation of population sizes of intertidal and subtidal habitats between both regions of the Dutch Wadden Sea exist, densities of shore crabs on intertidal flats should also be similar between the two areas.

Focussing on the Dutch Wadden Sea, the previously described higher abundances of shellfish-eating birds in the western Dutch Wadden Sea add to the hydrodynamical conditions that are less favourable for mussel beds in the western Dutch Wadden Sea (see Donker 2015, for details). Unsurprisingly, the surface area of intertidal flats occupied by epibenthic bivalve beds in the western Dutch Wadden Sea is relatively low compared to the eastern Dutch Wadden Sea (Folmer et al. 2014, Donker 2015).

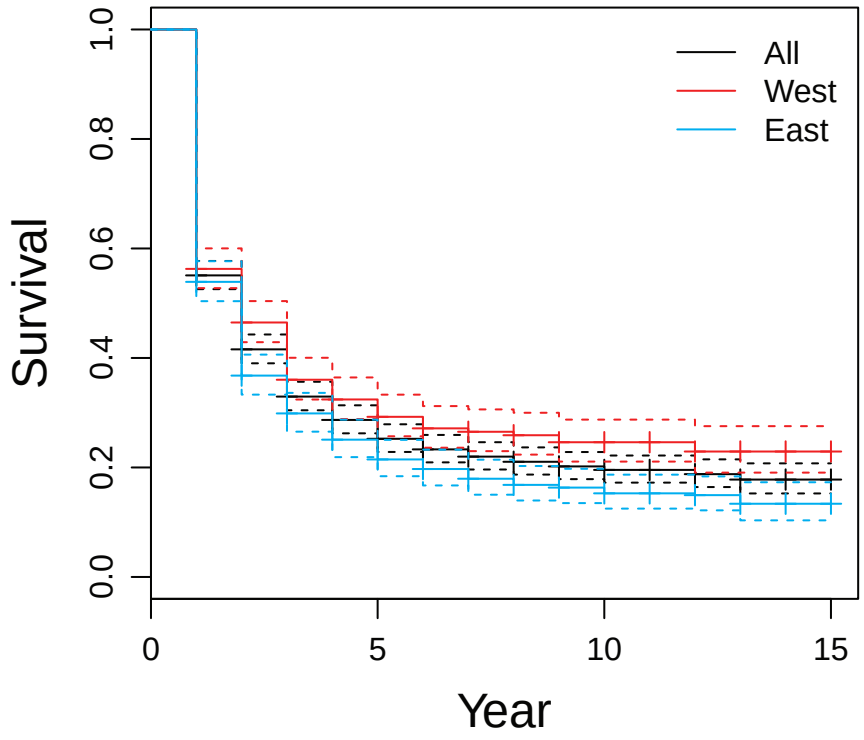

Figure 9.1: Comparison of survival curves of bivalve beds in the eastern and western Dutch Wadden Sea for the period 1999–2013. Analysis similar as described in Chapter 3. Dashed lines show average ± SEs.

This low bivalve bed area might be a result of low establishment or high loss rates of the bivalve beds. A survival analysis similar to the one described in **Chapter 3**, however, could not verify high loss rates in the west and instead indicated a slightly higher bivalve bed survival in the western Dutch Wadden Sea compared to the eastern Dutch Wadden Sea (van der Meer et al. unpublished data, Figure 9.1). This analysis, however, only considers beds that already survived the first year. Hence, less suitable conditions during the earlier establishment phase of bivalve beds, such as hydrodynamics (Donker 2015) or predation on post settlers (by e.g. shrimps and juvenile shore crabs; Reise 1985, Andresen 2013, Beukema & Dekker 2014), might be the primary reason for the sparse occurrence of bivalve beds in the western Dutch Wadden Sea.

Importance of parasitism in intertidal shore crab populations

The comparably high survival of established bivalve beds in the western Dutch Wadden Sea contradicts the observations of adverse hydrodynamical conditions and of high predation pressures exerted by shellfish-eating birds. This suggests that also other factors might be important with respect to the persistence of intertidal bivalve beds. Besides the numerical abundances, also the food demands of predators are important in governing the predation

pressure on a given prey item. A factor that can have crucial impacts on the feeding rates of crustacean predators is the infestation with parasites (Dick et al. 2010, Haddaway et al. 2012, Toscano et al. 2014). For example, acanthocephalan infection resulted in an increased feeding of up to 30% in the gammarid hosts (Dick et al. 2010), while infection with rhizocephalan parasites caused a reduction in feeding rates of up to 75% in brachyuran crabs (Toscano et al. 2014). In the Dutch Wadden Sea, the shore crab *Carcinus maenas*, one of the most notable predators on intertidal mussels, was found to be infested with four parasite species of three different taxonomic groups (acanthocephalans: *Profilicollis botulus*; microphallid trematodes: *Maritrema subdolum* and *Microphallus claviformis*; rhizocephalans: *Sacculina carcini*). While a considerable portion of *C. maenas* was found to be infested with acanthocephalans (~50%) and trematodes (~30%), prevalences of crabs infected with *S. carcini* were low (**Chapter 7** and **Chapter 8**). However, to what extent infection rates with these parasites differ between the western and eastern part of the Dutch Wadden Sea is still uncertain. Only the infection with the rhizocephalan *S. carcini* was assessed in both areas, indicating no substantial differences between west and east but an increased infection rate in subtidal areas (**Chapter 7**). The low infection rates with rhizocephalans and trematodes in the area corroborate studies on the feeding behaviour of *C. maenas* showing that rhizocephalan- and trematode infection both have little effects on the crabs feeding ecology (Larsen et al. 2013, Blakeslee et al. 2015). In contrast, little is known on the impact of acanthocephalans, and the fact that about half of the investigated shore crabs were found to be infected with these parasites shows the urgent need for further studies to clarify the effects of acanthocephalan infection on the feeding ecology of *C. maenas*.

Pacific oysters and their impact on bed survival

Another possible reason for differences in bivalve bed survival between the western and eastern Dutch Wadden Sea could be based on considerable regional differences in bivalve bed composition. After the collapse of intertidal mussel beds in the early 1990s (Figure 1.2), the recolonization of the intertidal by mussels differed between the western and eastern part of the Dutch Wadden Sea. While many intertidal areas of the eastern Dutch Wadden Sea readily got recolonized by mussels (e.g., Dankers et al. 2001), re-establishment of mussel beds in the western Dutch Wadden Sea remained very low. Yet, many intertidal areas of the western Dutch Wadden Sea, formerly occupied by mussels, were colonized by Pacific oysters, which settled on shell debris of the former mussel beds. Consequently, bivalve beds differed in their composition between the western and eastern Dutch Wadden Sea, with a low fraction of pure mussel beds in the west and high portions of this bed type in the east (van Stralen et al. 2012, Figure 9.2). Interestingly, pure mussel beds exhibit a lower persistence compared to beds occupied by Pacific oysters (Reise et al. 2017b, **Chapter 3**).

The higher survival of beds rich in Pacific oysters is due to the permanent anchorage of the oysters, resulting in rigid and persistent structures (Walles et al. 2015a). In contrast, mussels are temporarily attached via byssus threads and are vulnerable to harsh environmental conditions, such as storms and ice scouring (Nehls & Thiel 1993, Strasser et al. 2001, Donker 2015). Furthermore, *C. gigas* are less prone to predation compared to mussels, as primarily small oysters are preyed upon and larger specimens are only taken sporadically (Dare et al. 1983, Mascaró & Seed 2001a, Cadée 2001; 2008b;a, Markert et al. 2013, Weerman et al. 2014).

Initial concerns that Pacific oysters may outcompete the native mussels (e.g., Troost 2010) seem not to come true, as both bivalve species are found to coexist at many locations throughout the Wadden Sea (Markert et al. 2013, Reise et al. 2017b;a, Figure 1.2) and elsewhere in Europe (Groslier 2014, Holm et al. 2015; 2016, Norling et al. 2015, Herbert et al. 2016). Moreover, mussels may take advantage of the biocenosis with the alien oyster by settling in the inter-spaces between adult oysters (Buschbaum et al. 2016, Reise et al. 2017b) and thereby gaining shelter from harsh environmental conditions and from predation. For example, mussels cohabiting with oysters are

less prone to predation by shore crabs (Eschweiler & Christensen 2011, **Chapter 6**). Moreover, bivalve beds rich in Pacific oysters are less attractive foraging grounds for shellfish-eating birds (Markert et al. 2013, **Chapter 4**), due to reductions in the accessibility (**Chapter 6**) and body condition (**Chapter 4**) of the mussels.

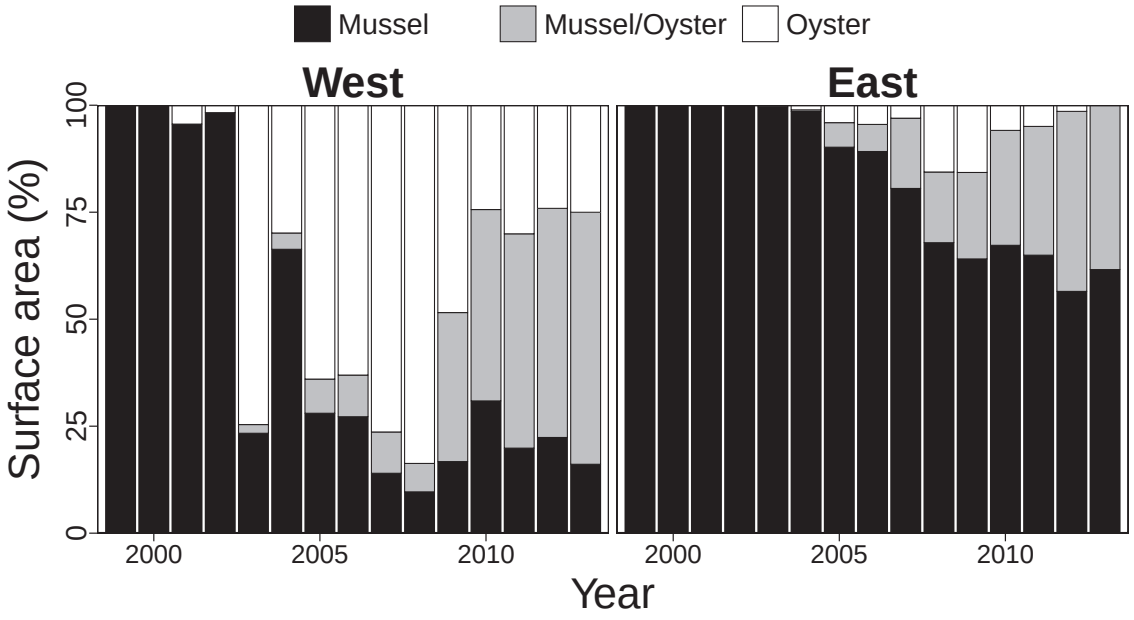

Figure 9.2: Surface area (%) of the different types of bivalve beds in the western and eastern Dutch Wadden Sea in the period 1999–2013. Plots based on surface area (ha) data from CBS et al. (2017).

Consequently, differences in persistence between beds differing in bivalve composition were also apparent in the comprehensive surveys of a selection of bivalve beds throughout the Dutch Wadden Sea in the years 2010–2013. These surveys were initially designed to follow the fate of newly established beds. But low recruitment resulted in only one new bed (W001_A1) in the entire Dutch Wadden Sea, so that the surveys were conducted mostly on perennial beds. The surveys showed that beds with many Pacific oysters remained fairly consistent in their areal extent over a period of three years, corroborating the findings of the long-term study of intertidal beds in the entire Dutch Wadden Sea for the period 1999-2013 (**Chapter 3**). In contrast, pure mussel beds, commonly showed a gradual decrease in bed area and/or a thinning in mussel coverage throughout the study period. This gradual decrease in mussel area, is to a certain extend based on the intense predation pressure on the mussels. For example, on the bivalve bed W001_A1, the average annual predation pressure on the macrobenthos exerted by mussel-eating birds in the period 2010–2013 accounted for about 680 kg AFDM per hectare bivalve bed (Table 9.1) and exceeded the secondary production of the dominating mussel cohort from 2009 (average annual production ca. 250 kg AFDM ha^{-1}, Table B3.1). Due to this high predation pressure, the mussel population is subject to drastic depletion and density decreases over time, if no substantial new spatfall occurs (Figure B3.1, Figure B3.2). In contrast, beds rich in Pacific oysters, show much lower abundances of shellfish-eating birds (**Chapter 4**), resulting in a reduced depletion of the mussels.

Crab predation and its potential impact on mussel recruitment

Hence, replenishment of the mussel population by regular recruitment events is of particular importance for pure mussel beds in order to balance the depletion of older specimens and to persist over long time periods. However, mussel recruitment on the intertidal beds often is insufficient to compensate the losses and rejuvenate the existing mussel population (see

Table 9.1: Estimated average predation pressure during summer (May–October) and winter (November–April) on macrobenthos by molluscivorous birds on the bivalve bed W001_A1 for the period 2010–2013. All mass indications refer to ash free dry mass (AFDM) measurements.

			Daily		Consumption	
Season	**Species**	**Mass (g ; g AFDM [a])**	**consumption ($g\ d^{-1}$)**	**Density ($n\ ha^{-1}$)**	**Daily ($kg\ ha^{-1}d^{-1}$)**	**Total ($kg\ ha^{-1}$)**
Summer	Oystercatcher	544 [b]; 184	43 [e]	29.55 [h]	1.27	231.1
	Eider	2162 [c]; 730	143 [f]	4.91 [i]	0.7	127.4
	Herring Gull	944 [d]; 319	66 [g]	4.83 [j]	0.32	58.2
	Sum					416.7
Winter	Oystercatcher	593 [b]; 200	52 [e]	18.2 [h]	0.95	172.9
	Eider	2162 [c]; 730	177 [f]	2.36 [i]	0.42	76.4
	Herring Gull	944 [d]; 319	66 [g]	1.26 [j]	0.08	14.6
	Sum					263.9
Total sum						680.6

[a] mass conversion: $y = 0.3378x$, with y = ash free dry mass (AFDM) and x = wet mass (WM); after Horn & de la Vega (2016)
[b] seasonal data in the Wadden Sea from Fig. 15 in Zwarts et al. (1996b)
[c] data: shot birds in the Wadden Sea from Chapter 6 of Kats (2007); no seasonal specific information available
[d] after Appendix 10 from Camphuysen (2013); no seasonal specific information available
[e] after Hilgerloh (1997)
[f] based on monthly data from Nehls (1995)
[g] daily requirements: (1462.5 kJ, Camphuysen 2013); conversion energy to biomass: (22 kJ per g AFDM, Zwarts et al. 1996a)
[h] data: seasonal trend of bird numbers on bed W001_A1 (6.8 ha) in Figure S4.7
[i] data: seasonal trend of bird numbers on bed W001_A1 (6.8 ha) in Figure S4.6
[j] data: seasonal trend of bird numbers on bed W001_A1 (6.8 ha) in Figure S4.23

Table 9.2: Estimated predation pressure during summer (May–October) on macrobenthos by shore crabs of varying sizes on the bivalve bed W001_A1. Abundance estimates are based on sampling in 2012–2013 and 2012 for juveniles and adults, respectively. All consumption figures refer to 15 °C, which is the mean sea surface temperature (SST) for the period May–October in the western Dutch Wadden sea (van Aken 2008b). Consumption at 15 °C was calculated based on life-stage dependent feeding rates measured at slightly higher temperatures (17 °C and 20 °C) and a Q10 value of 2.11 (*C. maenas* for 15–22 °C; Robertson et al. 2002). All mass indications refer to ash free dry mass (AFDM) measurements.

Size (mm CW)	**Mass (g)**	**Daily consumption ($g\ d^{-1}$)**	**Density ($n\ ha^{-1}$)**	**Consumption ($kg\ ha^{-1}d^{-1}$)**	**Consumption ($kg\ ha^{-1}$)**
Small (8.5)	0.03 [a]	0.005 [c]	168000 [e]	0.76	138.6
Medium (42.5)	3.09 [b]	0.124 [d]	184.14 [f]	0.02	4.2
Big (57.5)	7.92 [b]	0.411 [d]	142.94 [f]	0.06	10.7
Sum					153.5

[a] crabs < 20 mm CW: $\log y = -1.2557 + 2.8573 \log x$, with y = ash free dry mass (AFDM, mg) and x = carapace width (mm) after Klein Breteler (1975a)
[b] crabs > 20 mm CW: $\log y = -1.57709 + 3.112 \log x$, with y = ash free dry mass (AFDM, mg) and x = carapace width (mm) after Afman (1980)
[c] juveniles (< 20 mm CW) at 20 °C;: $\log y = -0.2152 + 0.7383 \log x$, with y = daily consumption (mg) and x = ash free dry mass (AFDM, mg) after Klein Breteler (1975a)
[d] adult males (> 20 mm CW) at 17 °C: $y = 17.56 + 4.88x$, where y = feeding rate in kJ and x = carapace width in cm after Elner (1980); conversion energy to biomass (22 kJ per g AFDM) after Zwarts et al. (1996a)
[e] data: ~ 140 crabs m^{-2} on bivalve covered patches (Figure B5.1); bivalve cover ~ 12% = 168000 crabs per ha bivalve bed
[f] abundance calculations after Chapter 5

Table 9.3: Comparison of predation pressure on intertidal mussels at bed W001_A1 exerted by shellfish-eating shorebirds and by shore crabs. Given are the predators annual consumption, prey size range and the daily intake rate. It has to be noted that for the birds daily intake rates were estimated on the basis of an entire year and for shore crabs only for the period May–October.

Predator	Annual consumption (kg AFDM ha^{-1})	Prey size (mm)	Prey mass (g AFDM [e])	Daily intake rate (m^{-2} d^{-1}) min	max
Oystercatcher	404	25–45 [a]	0.0693–0.3976	0.28	1.6
Eider	203.8	25–60 [a]	0.0693–0.9347	0.06	0.81
Herring Gull	72.8	10–20 [b]	0.0046–0.0357	0.59	4.56
Small crab	138.6	1–5 [c]	0.00002–0.0012	63.46	3807.69
Medium crab	4.2	5–15 [d]	0.0012–0.0152	0.15	1.92
Big crab	10.7	15–25 [d]	0.0152–0.0693	0.08	0.39

[a] (Bult et al. 2004) [b] (Camphuysen 2013) [c] (Mascaró & Seed 2001b) [d] (Mascaró & Seed 2001a)
[e] length-biomass relationship of juveniles (1–4 mm): $W = 18.8L^{2.6}$, where W = weight AFDM in µg and L = shell length in mm, after Riisgård et al. (1980); mussels (> 5 mm) at W001_A1 Waser unpubl.: $\log y = -5.313166 + 2.971523 \log x$, where y = mass AFDM (g); x = length (mm)

Box 3.1, Figure B3.1). Such low recruitment is often caused by high predation rates on the recently settled bivalves (Reise 1985, Andresen 2013, van der Heide et al. 2014). In the Wadden Sea, the main predators of post-settled bivalves are shrimps and juvenile crabs (Reise 1985, Andresen 2013, Beukema & Dekker 2014). Predation by shrimps on the macrobenthos can be substantial, causing high predation pressure on post-settling bivalves (e.g., Beukema & Dekker 2005, Andresen & van der Meer 2010, Jung et al. 2017). However, the extent of shrimp predation on juvenile mussels settling on the investigated bivalve beds is unknown, as densities of this mobile predator on the beds could not be quantified. In contrast, densities of juvenile shore crabs on the bivalve beds could be estimated from general bivalve surveys during low tide (Box 5.1). A rough estimate of potential predation pressure on mussels exerted by juvenile shore crabs (~ 8.5 mm CW) during summer (May–October) at bed W001_A1 is given in Table 9.2. Although these figures reflect a simplified picture of the abundance of juvenile crabs, as they are only based on four sampling occasions in spring and autumn of the years 2012 and 2013 (see Box 5.1), these figures still illustrate the considerable impact juvenile crabs may have on post-settling mussels with an estimated consumption of about 140 kg AFDM (Table 9.2) per hectare bivalve bed (this amounts to a daily intake rate of up 3808 mussels (size of 1 mm) per m^2; Table 9.3) in the period May–October. A thorough analysis of predation impact and hence density of juvenile crabs, however, would require more frequent sampling in order to capture differences in crab density and size distribution throughout the season (Klein Breteler 1976b, Beukema 1991, Moksnes 2002, Box 5.2, Figure B5.4). Another uncertainty is in the size preferences of these juvenile crabs. Although a few studies investigated size preferences of juvenile shore crabs preying upon mussels (Mascaró & Seed 2001b, Breen & Metaxas 2008, Morton & Harper 2008), none of these studies adequately investigated the size preferences of crabs as small as 8.5 mm CW. Hence, the prey range used for this crab size is ambiguous and could only be guessed from prey preferences of slightly bigger crabs (15–25 mm CW; Mascaró & Seed 2001b). A further factor, complicating the assessment of the impact of juveniles crabs on small mussels is in the difficulty of estimating ash free dry weight of small mussels. These very small mussels are only present on intertidal flats for a rather short time interval and are easily overlooked when sampling larger mussels, so that the very small individuals sampled on the bivalve beds are underrepresented (Figure B3.1, Figure B3.2). Since small mussels have a higher flesh to shell ratio, and hence, a higher body mass index (BMI) than bigger specimens (Rob Dekker pers. communication, own observation), extrapolation of the length-weight relationship of bigger mussels results in underestimation of the biomass of the very small mussels. To overcome this

problem, length-weight relationships focussing on these small mussels were taken from the literature (Riisgård et al. 1980). However, the estimated amount of mussels with a length of 1 mm eaten per in a m^2 bivalve bed per day (3808; Table 9.3) seems rather high, suggesting an underestimation of mussel biomass as a potential source of error.

Juvenile mussels may further be subject to predation by two introduced small crab species: the Asian shore crab (*Hemigrapsus sanguineus*) and the brush-clawed shore crab (*Hemigrapsus takanoi*), which both occupy similar habitats as *C. maenas* (Box 5.1, **Chapter 8**). Studies on the feeding ecology on these crabs are scarce, with only a few conducted with *H. sanguineus* on the US East Coast (e.g., Brousseau et al. 2001, Lohrer & Whitlatch 2002, Griffen et al. 2015). These studies showed that *H. sanguineus* readily feeds on juvenile *M. edulis*. Further studies are needed to determine size-specific energy demands and prey-size preferences of both *Hemigrapsus* species. Based on low tide sampling in 2012 and 2013, densities of about 20 *Hemigrapsus* spp. (majority: *H. takanoi*) per m^2 bivalve bed could be determined for bed W001_A1. Assuming that these crabs have similar energetic requirements as juvenile *C. maenas*, *Hemigrapsus* spp. exerts predation pressures of about 20 kg AFDM ha^{-1} on the macrobenthos during summer time.

Concerning the predation pressure on mussels exerted by adult shore crabs, crab abundance on the bivalve beds was assessed indirectly by a combination of baited trap arrays on the beds with beam trawling along the bed contours (see **Chapter 5**). These efforts were made in June and it must be further tested if the attained relationship between trap catches on the beds and crab abundance on the surrounding bare flats can also be used to convert trap catches made earlier or later in the season. Repeated deployment of crab traps on the bivalve bed W001_A1 indicated that the rate of medium sized crabs caught in the traps changed throughout the season (see Box 5.2, Figure B5.3), suggesting that the relationship of the two methods attained in **Chapter 5** is less suited to estimate crab abundance throughout the year. Therefore, the estimate of crab abundance used to calculate the predation pressure on the mussels was solely based on one sampling event from early summer (**Chapter 5**). It is assumed that the resulting density estimates reliably reflect average crab densities during summer periods, so that the estimated predation pressures of 15 kg AFDM (4.2 and 10.7 kg AFDM ha^{-1} for medium (42.5 mm CW) and big crabs (57.5 mm CW), respectively, Table 9.2) per hectare bivalve bed should be more or less representative. Crabs are known to select mussel sizes that pose the lowest risks for claw damage (Elner & Hughes 1978, Smallegange & van der Meer 2003). Hence, adult crabs preferably prey on juvenile mussels, not exceeding shell lengths of 25 mm, that can easily be crushed with their claws. The daily intake rates during summer achieved on bed W001_A1 by adult crabs amount up to 1.9 and 0.4 mussels per m^2 for medium and big crabs, respectively (Table 9.3). The figures illustrate that crab predation in combination with the predation exerted by Herring Gulls (4.6 $m^{-2}d^{-1}$, Table 9.3), which similarly prey on juvenile mussels, may play important roles in the survival of young mussels of 0–2 years of age. Older mussels, well above shell lengths of 25 mm are preyed upon by Oystercatcher and Common Eider. As these larger mussels have higher biomasses, the maximum daily intake rates of the birds are with 1.6 (Oystercatcher) and 0.8 (Eider) (Table 9.3) lower than the rates achieved of the Gulls and crabs on the smaller mussels.

In order to be able to quantify differences in predation pressure among bivalve beds differing in the bivalve composition, detailed information on the mussel population as well as on the predators are required. In this thesis, first attempts towards a quantification of the predation pressure on mussels on different types of bivalve beds have been performed. Several important drawbacks became apparent, which make the comparison of predation pressure among different types of bivalve beds extremely difficult. Besides the difficulties in estimating the predation pressure on mussels by shore crabs, further restrictions were observed concerning the classification of mussels into different age cohorts. Particularly on oyster dominated beds, mussels showed a high variability in shell length, which made it impossible to follow cohorts through time (Box 3.1). Even for pure mussel beds, the assignment into cohorts was not without difficulty, as the recruitment of mussels showed irregular patterns. For example, it seems that in

the year 2011 several spawning events occurred on the bivalve bed W001_A1, as more than one new size mode emerged (see Figure B3.2).

Implications for mussel bed restoration

In the past, many attempts to restore intertidal mussel beds proved unsuccessful (Capelle et al. 2014, Dankers & Fey-Hofstede 2015, de Paoli et al. 2015). These restoration efforts often comprised the relaying of fished subtidal mussels in varying densities on the intertidal flats. In most cases these man-made mussel beds disappeared shortly after they had been created. The low success rate of this procedure is attributed to the subtidal origin of the mussels, as these mussels are barely capable to withstand the harsh conditions in intertidal areas (hydrodynamics, predators; de Paoli 2017). Earlier work showed that bed survival can be increased severalfold, when instead of subtidal mussels, intertidal mussels are used for the creation of beds (Donker 2015, de Paoli 2017). Yet, destroying natural intertidal mussel beds to restore mussel beds elsewhere on the intertidal is not a viable option.

An alternative to transplanting mussels is the enhancement of larval settlement onto the intertidal flats. Analogous to the restoration of oyster reefs (e.g., Nestlerode et al. 2007, George et al. 2015), the provision of settlement structures may facilitate mussel recruitment by significantly reducing predation on post-settling mussels. In the Dutch Wadden Sea, recent mussel bed restoration efforts focussed on the viability of Biodegradable Elements for Starting Ecosystems (BESE). These structures are made of starch from potato waste and offer settlement surface and predation refuge for settling mussel larvae. These structures are assumed to entirely decompose, leaving behind a functional mussel bed with plentiful adult mussels. However, it is not known how long it will take for the structures to decompose. On the basis of assumptions, not measurements, it is estimated that the structures will survive at most 10 years until fully decomposed. Furthermore, it remains to be seen how mussels settling on these structures will perform in the long run and whether these structures indeed are suitable alternatives in restoring mussel beds.

An alternative to the use of the plastic-like BESE structures may be offered by Pacific oysters inhabiting the Wadden Sea. This thesis demonstrates that mixtures of mussels and Pacific oysters show a much higher survival in comparison to pure mussel beds (see also Reise et al. 2017b). Consequently, employment of Pacific oysters in restoration measures should enhance the likelihood that man-made structures persist over long time periods. In the Dutch Wadden Sea, there are no experiences with man-made aggregations of both Pacific oysters and mussels. However, such constructions proved to be successful in the Northern Wadden Sea near the island Sylt, where six 10 × 10 m squares of a mixture of mussels and Pacific oysters, constructed in summer 2008, persisted over several years and remained fairly stable with only minor losses in surface area (Reise et al. 2017a). It seems likely that created structures of mixed oysters and mussels would also persist over long time periods in the Dutch Wadden Sea. However, future work is needed to find out the best options for creating such mixed bivalve beds. To avoid fishing up intertidal beds consisting of established Pacific oysters, alternatives would be to use oysters of subtidal origin or the use of oyster shells to create artificial reefs (e.g., Walles et al. 2016).

From an ecological perspective the term 'mussel bed' seems largely outdated, as many beds in the Dutch Wadden Sea nowadays are a mixture of mussels and Pacific oysters. Pure mussels beds seem to be restricted to higher parts in the tidal zone (see Figure 4.2). It is uncertain if these pure beds will persist in the future, as recent monitoring data indicate the proliferation of oysters and the change into mixed beds is still ongoing (Figure 1.2). As Pacific oysters became established in the Wadden Sea and are now ineradicable, mixed beds of oysters and mussels should be accepted as a historical contingency (Reise et al. 2017b) and should be seen as a vital addition to the habitat complexes within the Wadden Sea (e.g., Ssymank & Dankers 1996).